

**Abstract.**—Growth parameter estimates were calculated for the tiger shark (*Galeocerdo cuvier*) by using tag and recapture data. Results were compared to published estimates based on bands in vertebrae. The von Bertalanffy parameters (sexes combined) based on tag and recapture growth data were as follows:  $L_{\infty} = 337$  cm fork length,  $k = 0.178$ , and  $t_0 = -1.12$ . Monthly length-frequency data for six year classes from birth to two years old for tiger sharks were used to verify the tag-recapture growth curve for this age range. The predicted age at maturity is 7 years for both sexes. Data from an ongoing *in situ* study with oxytetracycline were used in conjunction with length data to determine the effect of tagging and oxytetracycline injection on growth. The data suggest that tagging alone or tagging combined with oxytetracycline injection has little or no effect on the growth rate of tiger sharks up to two years of age.

## Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging

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Adult tiger sharks, *Galeocerdo cuvier*, occur worldwide in temperate and tropical coastal waters. In the North Atlantic, they reside year round off the coast of Florida and seasonally migrate north as far as Nova Scotia, Canada (Kohler et al., 1995). Additionally, tiger sharks are known to make extensive migrations throughout the North Atlantic, on occasion traveling to Cuba and Africa.<sup>1</sup> The tiger shark is listed under the large coastal shark category of the Fisheries Management Plan for Sharks of the Atlantic Ocean (Anonymous, 1993). Although it is not a target species of the U.S. inshore longline fishery, small tiger sharks are frequently caught and released alive. Tagging and fishery data indicate that there is a nursery ground for tiger sharks on the continental shelf off the southeast coast of the US.<sup>1</sup> This area extends from about Augusta, GA, to Daytona, FL, and extends from shore seaward to depths of 100 m. A similar area exists off the coast of North Carolina.<sup>2</sup> In these areas, tiger sharks of birth size ranging from 61 cm fork length [FL]) to 120 cm FL are commonly

caught in the commercial longline fishery. In the Northwest Atlantic, tiger sharks mature between 258 and 265 cm FL (Branstetter et al., 1987) and have been reported to attain a size of 469 cm FL (Castro, 1983).

Branstetter et al. (1987) used the alternating opaque and translucent bands formed in the vertebral centra to age tiger sharks caught in the western North Atlantic and the Gulf of Mexico. Attempts to verify these estimates with length-frequency analysis proved unsuccessful owing to the inability to distinguish age groups. Branstetter et al. (1987) tried to corroborate the vertebrally derived growth rate with results from one tag-recapture individual; however, this individual's length was estimated at both tagging and recapture. Owing to the high age estimates at  $L_{\infty}$ , Branstetter et al. (1987) suggested that as tiger

<sup>1</sup> 1992–98. Apex Predators Program, 28 Tarzwell Dr. Narragansett, RI 02882. NMFS unpub. data.

<sup>2</sup> Chris Jensen. 1994. Natl. Mar. Fish. Serv. NOAA, 28 Tarzwell Dr., Narragansett, RI 02882. Personal Commun.

sharks approach maximum sizes, their vertebrae and band deposition may not reflect age. Because attempts at verification were unsuccessful, and direct validation was not possible, the determination of the tiger shark growth rate was not completely satisfied.

To determine if vertebral growth bands reflect age in older individuals and possibly to verify the estimates of Branstetter et al. (1987), we undertook a study with tag and recapture data to estimate, independently, von Bertalanffy parameters for the tiger shark. Verification of neonatal and juvenile growth rates was accomplished by using monthly length-frequency data obtained over a period of seven years. In addition, data on growth of oxytetracycline (OTC)-injected tagged and released tiger sharks from an ongoing study were available to compare with length-frequency and tagging growth data.

## Materials and methods

Data from tiger sharks were obtained between 1963 and 1997 from research vessel cruises, sportfishing tournaments, and the commercial shark fishery from Cape Cod, MA, to the Florida east coast. Data for monthly length-frequency analyses were obtained from tiger sharks caught by longline in a delineated area within the nursery grounds off Florida during 1988–94 (Fig. 1).

### Length measurements

Measurements of total length (TL) and FL were taken to the nearest centimeter (cm) following the conventions of Bigelow and Schroeder (1948). Fork lengths are reported unless otherwise noted. TL to FL conversions can be calculated from the relationship

$$FL = (TL \times 0.8761) - 13.3535 \quad r^2 = 0.99 \quad n=44$$

(Kohler et al., 1995)

### Tag-recapture data

During 1962–96, over 6000 tiger sharks were tagged with NMFS tags (Casey, 1985) and released as part of the NMFS Cooperative Shark Tagging Program. Tags were returned primarily by sport and commer-

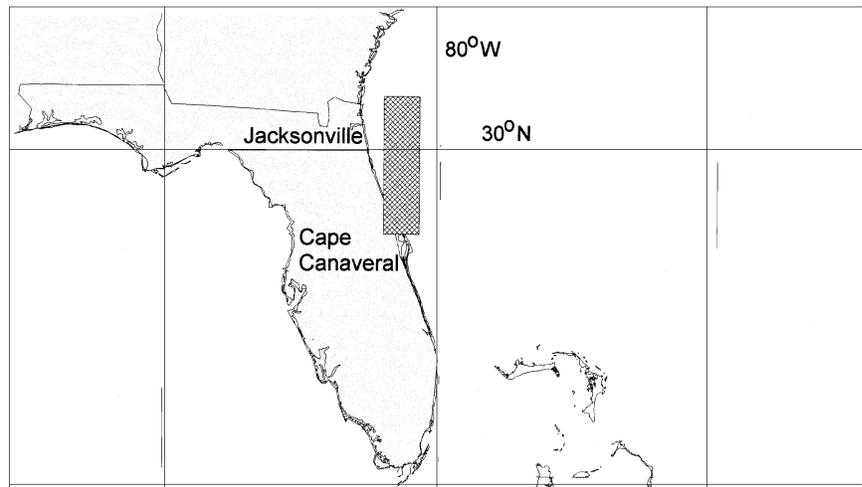


Figure 1

Map showing the portion of the nursery area (shaded box) from which monthly length-frequency samples were obtained.

cial fishermen who also reported shark size in TL, FL, or weight. All measurements and estimates were converted to FL.

Gulland and Holt's (1959) and Fabens' (1965) methods were used to calculate von Bertalanffy (1938) growth parameters from the tag-recapture data. Techniques for calculating the parameters according to Gulland and Holt (1959) came primarily from their publication and additional clarification was obtained from Cailliet et al. (1992). Only fish that were measured at both release and recapture and at liberty for at least 0.9 years were included in the analysis. Two of the three parameters for the von Bertalanffy (1938) growth function (VBGF),  $k$  and  $L_\infty$ , were estimated directly with the methods of Fabens (1965) and Gulland and Holt (1959).  $T_0$  cannot be estimated from tagging data alone, rather it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VBGF and solving for  $t_0$ , such that

$$t_0 = t + (1/k) \left[ \ln \left\{ (L_\infty - L_t) / L_\infty \right\} \right],$$

where  $L_t$  = known length at age (size at birth);  
 $k$  = the von Bertalanffy growth constant;  
 and  
 $L_\infty$  = the theoretical maximum attainable length from the VBGF.

The  $t_0$  values were calculated based on an average size at birth of 61 cm FL<sup>1</sup> with  $t = 0$ .

Longevity was estimated from the FL at which >99% of the  $L_\infty$  was reached (i.e.  $7 \ln 2 / k$ ) (Fabens, 1965; Cailliet et al., 1992). The von Bertalanffy parameters derived from these methods were compared with growth information obtained from the length-

frequency analysis. No OTC-injected individuals were included in these calculations.

### Tag-recapture with OTC injection

During 1985–97, more than 650 tiger sharks (59 to 291 cm FL) were measured, injected with a 25 mg/kg body weight dose of OTC (Gruber and Stout, 1983), tagged, and released. To determine the effects of OTC on growth, data from recaptured OTC-injected fish were analyzed separately from those of noninjected recaptured fish. Only those OTC-injected specimens measured at both tagging and recapture and at liberty for at least 0.9 years were included in the analysis. For comparison of growth of injected fish to growth of noninjected fish, the growth rates from OTC-injected individuals were plotted with the von Bertalanffy growth function (VBGF) from the tag-recapture analysis. The size at tagging was used as a guide to estimate age at tagging with the VBGF. The time at liberty determined the distance along the  $x$ -axis, and sizes at recapture determined the slope. The growth of the OTC-injected individuals was then compared graphically with the growth curves for long-term (>0.9 yr) tag-recaptured sharks and monthly growth estimates.

### Monthly growth

Data for tiger sharks measured and subsequently tagged from the defined nursery area were analyzed for monthly growth. Data on measured fish were available by month from June 1988 to August 1994. Data were organized into 5-cm intervals. The modes for the 1988, 1989, 1990, 1991, 1992, and 1993 year classes were followed progressively from the birth mode until the last visible mode for that year class. Where modes were not clear (i.e. single fish at more than one interval) the mean was taken as the mode. Previously tagged individuals were not included in this data set. Length-frequency histograms were developed for each month of each year for modal analysis. To determine if the data from the six year classes could be combined, the modes of each year class were plotted by month and compared graphically and through an analysis of covariance. Growth per year was calculated by subtracting the June birth mode from the June one-year mode and the June one-year mode from the June second-year mode. To compare the growth of these fish to tagged noninjected fish and tag-recaptured OTC-injected fish, month-per-year growth rates were plotted against the VBGF from the recapture analysis and the growth rates from the individual tag-recaptured OTC-injected fish. The initial positioning of the modes on the  $x$ -axis assumes birth takes place in June<sup>1</sup> so that the first

point of the monthly growth was fixed on the monthly tag-recapture curve for June. The monthly growth values were fixed on the curve on the basis of month they were calculated for (i.e. June, birth; June, year 1; June, year 2). Graphical comparisons enabled us to determine whether growth based on the tag-recapture analysis was distinct from growth based on a method without tagging (represented by monthly growth). In addition, we compared Branstetter et al.'s (1987) vertebral growth curve to these data.

## Results

### Tag-recapture data

Information on 42 recaptured tiger sharks, measured at both tagging and recapture and at liberty for at least 0.9 years, was used to produce values of  $L_{\infty}$  and  $k$  of the VBGF (Table 1). The Gulland and Holt (1959) method produced the most biologically plausible estimates of VBGF parameters (Table 2). The Fabens (1965) analysis underestimated  $L_{\infty}$  with known maximum size estimates, and the value for  $k$  was high. Therefore, further analysis was based on the results from the method of Gulland and Holt (1959). Age at maturity, based on lengths at maturity from Branstetter et al. (1987), for female (265 cm FL) and male (258 cm FL) tiger sharks is 7 years (Fig. 2; Table 3). Maximum age was estimated to be 27.3 years (335+ cm FL > 99% of  $L_{\infty}$ ).

### Tag-recapture with OTC injection

Analysis of the growth of the four OTC-injected specimens recaptured >0.9 years after tagging indicates that individuals grew at approximately the same rate as predicted by the tag-recapture data (Fig. 3). Growth calculated for the first year (growth/year of two individuals tagged at <100 cm FL) was 42.3 and 48.4 cm/yr. and 39.4 and 48.7 cm/yr. for the second year (growth/year two individuals tagged at >100 cm FL) (Table 1). These four individuals were at liberty between 0.94 and 1.19 years.

### Monthly growth

Modes were clearly visible in the length-frequency histograms for small tiger sharks of all year classes from birth to 1.5 years. The modes for 1.5–2 years were less distinct owing to decreased sample sizes at the larger sizes (Fig. 4). Differences in growth rates among the six year classes were statistically significant (ANCOVA,  $P>0.05$ ) so we did not combine the monthly length frequencies for all years (Fig. 4). In

the first year, the young grew from an average birth size of 65 cm FL to 100–105 cm FL with a growth rate of 40–45 cm/yr. (Fig. 4). More limited data on second year growth indicated a rate of 35–45 cm/yr. Even with this variation, growth in all years paralleled the tag-recapture growth curve and the individual growth rates of the OTC specimens (Fig. 3).

### Discussion

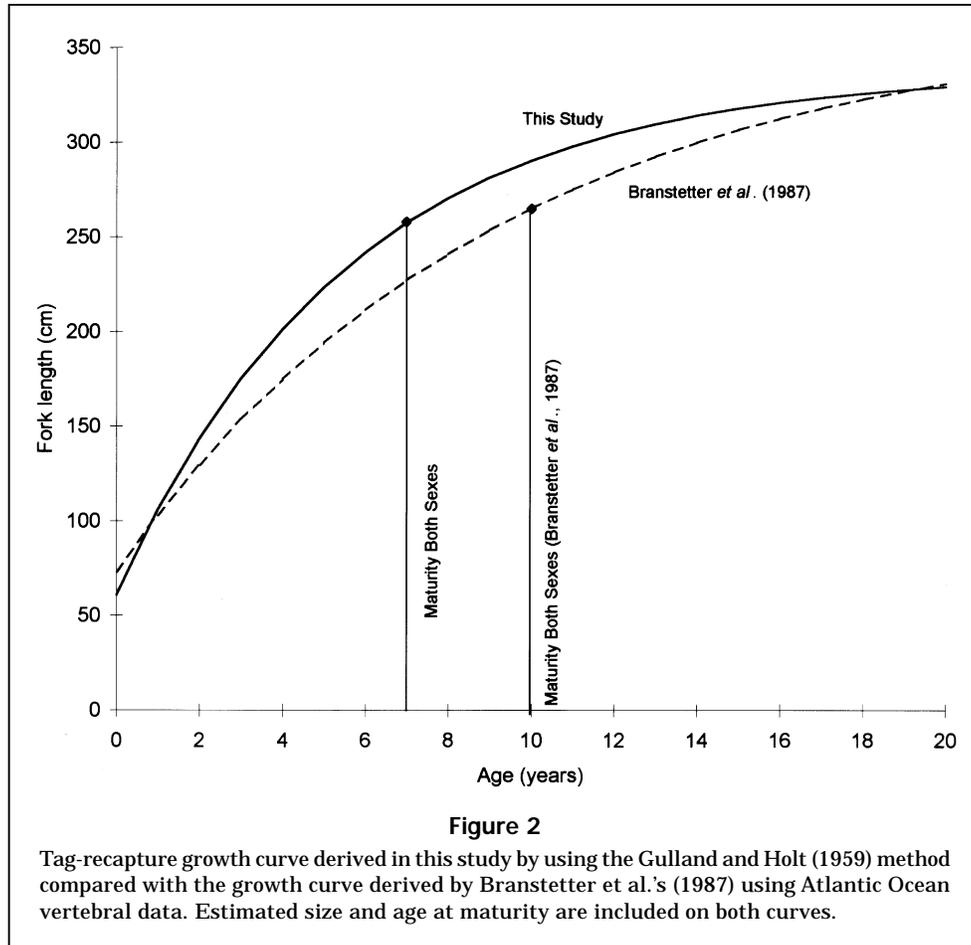
It is evident that traditional methods for aging teleosts do not always work well for sharks. Length-frequency analysis is difficult owing to the slow growth exhibited by most elasmobranch species. Hard part analysis requires validation of the periodicity of band formation, which is often difficult to obtain for shark species. Vertebral age estimates for the sandbar shark, *Carcharhinus plumbeus*, which was one of the six species considered validated, have been revised since Cailliet's (1990) paper by using tag and recapture evidence (Casey and Natanson, 1992). The new data indicate that although the vertebral bands may be formed annually in the young shark, as validated (Branstetter, 1987b), they are not formed annually throughout the life of the shark and, therefore, band counts severely underestimate age. This type of revision highlights the need for validation of all size classes. It is advisable to use several methods for aging to provide verification for the chosen growth curve, particularly if vertebral band counts are used without direct validation.

Tag-recapture data can be a useful tool for age and growth determination if accurate measurements are taken at both tagging and recapture and if individuals are at liberty for a sufficient time for growth to occur. However, problems are associated with this method as well. For example, most length measurements are estimated by recreational and commercial fishermen. For slow growing sharks, it is imperative to obtain accurate length measurements, particularly in large fish. This can prove difficult as well as dangerous at tagging. Therefore, data on large individuals is sometimes lacking and thus will bias results. Additionally, some researchers have shown that tagging with "M" type tags in small sharks, such as the lemon shark, may retard growth (Manire and Gruber, 1991). Analysis of the data can also be problematic. The Fabens (1965) method can lead to biased estimates because its basic premise, that tagged individuals are at large for equal time periods, is often violated with sharks. Estimates from that method lead to low values of  $L_{\infty}$  and high values of  $k$  (Chien and Condrey, 1987). The Gulland and Holt (1959) method, which allows for unequal times at liberty,

**Table 1**

Tag-recapture data used for growth and growth rate analyses. TAL = time at liberty, FLTAG = fork length at tagging, FLCAP = fork length at recapture,  $b$  = value calculated from Gulland and Holt (1959). Also shown are the data for the OTC-injected recaptured fish, although they were not included in growth analyses.

Id No.	Sex	TAL (yr)	FLTAG (cm)	FLCAP (cm)	Average growth/yr (cm)	$b$
1	M	4.02	75.0	222.0	36.5	0.26
2	F	1.39	76.0	122.0	33.1	0.09
3	M	1.69	76.2	111.8	21.0	0.11
4	F	0.90	77.0	124.0	52.3	0.06
5	F	1.42	78.7	114.3	25.1	0.09
6	F	1.75	79.0	136.0	32.5	0.12
7	M	0.97	85.0	130.0	46.6	0.06
8	F	1.60	86.0	171.0	53.0	0.11
9	F	1.22	88.0	128.0	32.8	0.08
10	F	0.91	89.0	120.0	34.0	0.06
11	F	0.92	90.0	155.0	70.9	0.06
12	F	4.90	91.0	211.0	24.5	0.32
13	M	1.00	91.0	122.0	30.9	0.07
14	F	4.90	91.0	211.0	24.5	0.32
15	M	2.04	91.0	168.0	37.7	0.13
16	F	1.03	94.0	136.5	41.2	0.07
17	F	1.60	96.0	157.0	38.1	0.11
18	M	1.01	97.0	147.0	49.5	0.07
19	F	1.51	98.0	154.0	37.0	0.10
20	M	0.97	98.0	142.0	45.4	0.06
21	F	3.28	98.0	195.0	29.6	0.22
22	F	0.95	102.0	157.0	57.9	0.06
23	F	0.90	104.0	124.0	22.1	0.06
24	M	0.99	106.0	156.0	50.4	0.07
25	M	1.00	106.0	160.0	54.2	0.07
26	M	1.37	108.0	147.0	28.4	0.09
27	F	0.97	109.0	160.0	52.6	0.06
28	F	1.07	110.0	173.5	59.6	0.07
29	M	0.94	111.0	156.0	47.9	0.06
30	F	1.56	114.0	155.0	26.2	0.10
31	F	2.20	117.0	184.0	30.5	0.14
32	F	1.69	117.5	175.5	34.3	0.11
33	M	0.90	118.0	152.0	37.7	0.06
34	M	1.48	120.0	167.0	31.8	0.10
35	M	0.91	121.0	161.0	43.9	0.06
36	F	1.37	124.0	173.0	35.7	0.09
37	M	0.91	124.0	137.0	14.2	0.06
38	F	0.93	149.0	164.0	16.2	0.06
39	M	1.16	170.0	193.6	20.3	0.08
40	F	5.28	190.0	235.0	8.5	0.35
41	F	1.20	281.0	288.0	5.8	0.08
42	M	3.33	287.0	317.5	9.2	0.22
218097	F	0.94	104.0	141.0	39.4	
304303	M	0.98	70.5	112.0	42.3	
190804	F	1.19	100.0	158.0	48.7	
204379	M	1.06	93.5	145.0	48.4	



**Table 2**

VBGF parameters calculated by using two different tag-recapture methods (Gulland and Holt, 1959, and Fabens, 1965) ( $n=42$ ) and compared with Branstetter et al.'s (1987) estimates derived from vertebral analysis (fork lengths calculated by using Branstetter et al.'s (1987) conversions).

Model	$L_{\infty}$	SE	$k$	SE	$t_0$
Gulland and Holt, 1959	337 FL	6.95	0.178	0.048	-1.12
Fabens, 1965	293 FL	19.10	0.217	0.031	-1.08
Branstetter et al., 1987					
Atlantic	440 TL ( 365 FL)	0.107	-2.35		
Gulf of Mexico	388 TL (324 FL)	0.184	-1.13		

therefore, appears to be more appropriate for sharks (Cailliet et al., 1992).

In this study, the Gulland and Holt (1959) method produced more biologically reasonable results than the Fabens (1965) method. The  $L_{\infty}$  calculated from the Gulland and Holt method was 337 cm FL, which is lower than the maximum reported western North Atlantic values from the literature (391 cm FL;

Bigelow and Schroeder, 1948). More recently, in the western North Atlantic and Gulf of Mexico, the largest sharks observed were 346 cm FL (Branstetter, 1981) and 339 cm FL<sup>3</sup> the latter quite close to our

<sup>3</sup> Kohler, N. E., H. W. Pratt Jr., L. J. Natanson, P. Turner, and R. Briggs. 1996. The shark tagger 1995 summary. Narragansett Laboratory, Northeast Fish. Science Center, Natl. Mar. Fish. Serv., NOAA, 16 p.

estimate. However, the tiger shark has been reported to 469 cm FL (Castro, 1983). The  $L_{\infty}$  value estimated from the Fabens (1956) method (293 cm FL), however, is lower than all reported values. In addition, the Fabens (1965) method value for  $k$  is high (Table 2). We therefore concluded that the Gulland and Holt (1959) VBGF is the more appropriate model to use for the tiger shark. Cailliet et al. (1992) and Van Dykhuizen and Mollet (1992) also preferred the Gulland and Holt (1959) model over that of Fabens (1965) for the angel and sevengill sharks, respectively.

Data from this study indicated that neither tagging nor tagging combined with OTC injection appears to retard the growth rate in neonate and juvenile sharks up to 150 cm FL (Fig. 3). To the contrary, the growth rates from tagged sharks were higher than estimates obtained from vertebral growth bands (Table 3). The growth rates for the first two years of life for the tiger shark estimated from monthly length frequencies, tag-recapture (Gulland and Holt, 1959), and tag-recapture with OTC were all similar (Fig. 3). Tanaka (1990) found that growth rates of OTC-injected Japanese wobbegongs, *Orectolobus japonicus*, and neonate swell sharks, *Cephaloscyllium umbratile*, were not significantly different from controls. More recently, Gelsleichter et al. (1998) evaluated the toxicity of OTC on growth rates of captive nurse sharks, *Ginglymostoma cirratum*, and concluded that there were no adverse effects of OTC on growth rate. These data support the use of OTC as an effective method for determining vertebral band periodicity without interrupting normal growth patterns (Tanaka, 1990; Gelsleichter et al., 1998).

Our data do not verify nor refute age estimates for the tiger shark previously obtained from vertebral band counts (Branstetter et al., 1987) (Table 2; Fig. 2). The  $k$  value from our study is higher than Branstetter et al.'s (1987) Atlantic value and our  $L_{\infty}$  is lower. These differences are to be expected when comparing VBGF parameters from a conventional age-length (vertebral methods) study with those derived from a growth increment (tagging) study (Sainsbury, 1980; Francis, 1988). These types of curves are not directly comparable because the parameters are derived differently and, therefore, have different meanings (Francis, 1988). However, comparison of the estimates obtained in these studies to known values, such as size at birth and maximum size, can provide insight into the fit of the curves. This information allows us to determine which curve is best suited to be used for age at maturity and maximum age estimates. We believe that the current tag-recapture values are more accurate on the basis of verification available from the monthly length-frequency analysis and the consistency of the estimates to measurable parameters such as size at birth and maximum size. The  $L_{\infty}$  calculated by Branstetter et al. (1987) is

**Table 3**

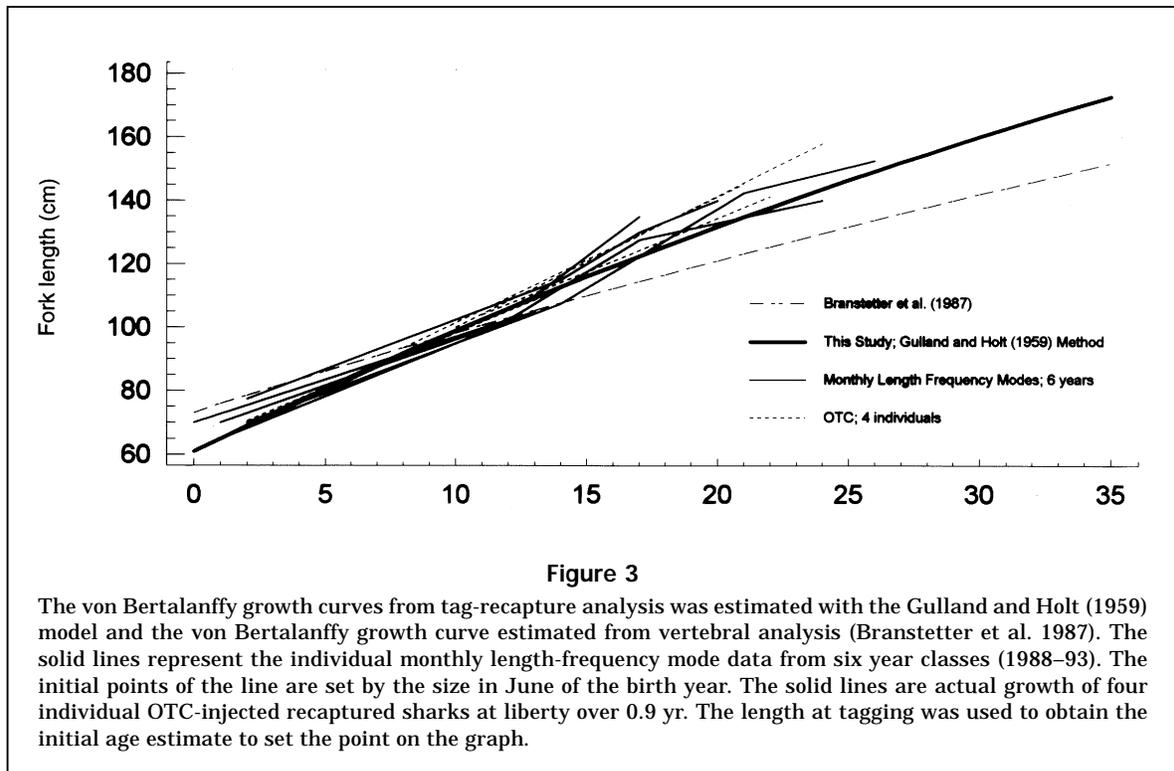
Size at age and growth per year for the tiger shark, *Galeocerdo cuvier*, calculated for tag and recapture data with Gulland and Holt's (1959) (this study) method compared with Branstetter et al.'s (1987) Atlantic vertebral data. Approximate size at maturity is indicated by bold typeface.

Age (years)	Size (cm, FL)		
	This study	Branstetter <sup>1</sup> 1987	This study growth/yr (cm)
Birth	61	73	
1	106	103	45
2	144	130	38
3	175	153	32
4	202	175	26
5	224	194	22
6	242	212	18
7	<b>258</b>	227	15
8	271	241	13
9	281	254	11
10	290	<b>265</b>	9
11	298	275	8
12	304	284	6
13	310	293	5
14	314	300	4
15	318	307	4
16	321	313	3
17	324	318	3
18	326	323	2
19	328	327	2
20	329	331	2

<sup>1</sup> Branstetter et al. (1987) values converted to FL.

lower than maximum reported sizes, and the size at birth (73 cm FL), based on the von Bertalanffy curve from that study, was high as related to known parameters (60–65 cm FL<sup>1</sup>).

Statistically significant differences between age estimates from the Gulf of Mexico and North Atlantic populations of tiger shark found by Branstetter et al. (1987) may not be biologically significant (Yoccoz, 1991). The differences in age at maturity obtained between these two areas is only 2–3 years. Considering the relatively slow growth and large overlap of size at age for this species, a 2–3 year difference could be included in the realm of measurement error. In addition, we found statistically significant differences in growth by year in first year tiger sharks obtained from the same region over a period of five years. The differences in growth between years indicate that tiger shark growth is quite variable and probably dependent on fluctuations of many parameters in-



cluding environmental conditions and prey availability. Our data show that the majority of neonatal tiger sharks remain in the nursery area from birth until about 120–150 cm FL or 1.5–2 years of age.<sup>1</sup> It is known that tiger sharks frequently migrate into and out of the Gulf of Mexico (Kohler et al., in press). It is doubtful, with the migratory nature of this species and mixing between these areas, that growth rate differences in these groups are biologically significant past perhaps the first three years of life.

The longevity of the tiger shark is difficult to estimate. The NMFS tagging program has received data on five tiger sharks at liberty for 6 to 11 years. The oldest of these fish would have been 3+ years at tagging (185 cm FL, estimated), on the basis of the Gulland and Holt (1959) growth curve and, therefore, 14+ years at recapture (325 cm FL, measured). Branstetter et al.'s (1987) oldest aged tiger shark was 16 years of age. Our longevity estimate, based on a 7 half-life criterion, indicated that tiger sharks may live to be at least 27 years of age. Branstetter et al. (1987) estimated maximum age at anywhere from 20–37 years based on  $L_{\infty}$  for their various VBGF curves and rate of growth of large individuals.

Based on revised growth estimates presented in this study, estimated maximum age for this species is 27 years. Age at maturity, estimated from tag-recapture data from this study and size at maturity estimates from Branstetter et al. (1987), is seven

years suggesting that females mature at 25% of their maximum age and may reproduce 10 times based on a two-year reproductive cycle.

Overall, the tiger shark is similar to other large carcharhinids in that it grows slowly and has a relatively long life, although it matures earlier than many other species in the northwest Atlantic (*C. leucas* 14–18 years, Branstetter and Stiles, 1987; *C. plumbeus* 15–30 years; Casey and Natanson, 1992, Sminkey and Musick, 1995; *C. obscurus* 19–20 years; Natanson, 1994; *C. falciformis* 6.5–12 years, Branstetter, 1987c, Bonfil et al., 1993). Branstetter (1987b) discussed the various life strategies of sharks on the basis of their  $k$  values. He suggested that tiger sharks, with  $k$  values from 0.11 to 0.16, fit into an intermediate category between slow growth species ( $k=0.05-0.10$ ) such as *C. plumbeus*, *C. obscurus*, *Negaprion brevirostris*, and *Sphyrna lewini* and fast growth species ( $k \geq 0.2$ ) such as *C. limbatus*, *C. brevipinna*, *Rhizoprionodon terraenovae*, and *Prionace glauca*. Other sharks in the intermediate group include *C. acronotus* and *C. falciformis* according to Branstetter (1987b). The tiger shark reaches maturity at a lower percent (25%) of its total age than do other carcharhinids for which this parameter has been estimated (*S. lewini* 33–50%, Branstetter, 1987c). This finding suggests that the tiger shark has a longer reproductive life span and possibly a greater reproductive potential than other carcharhinids.

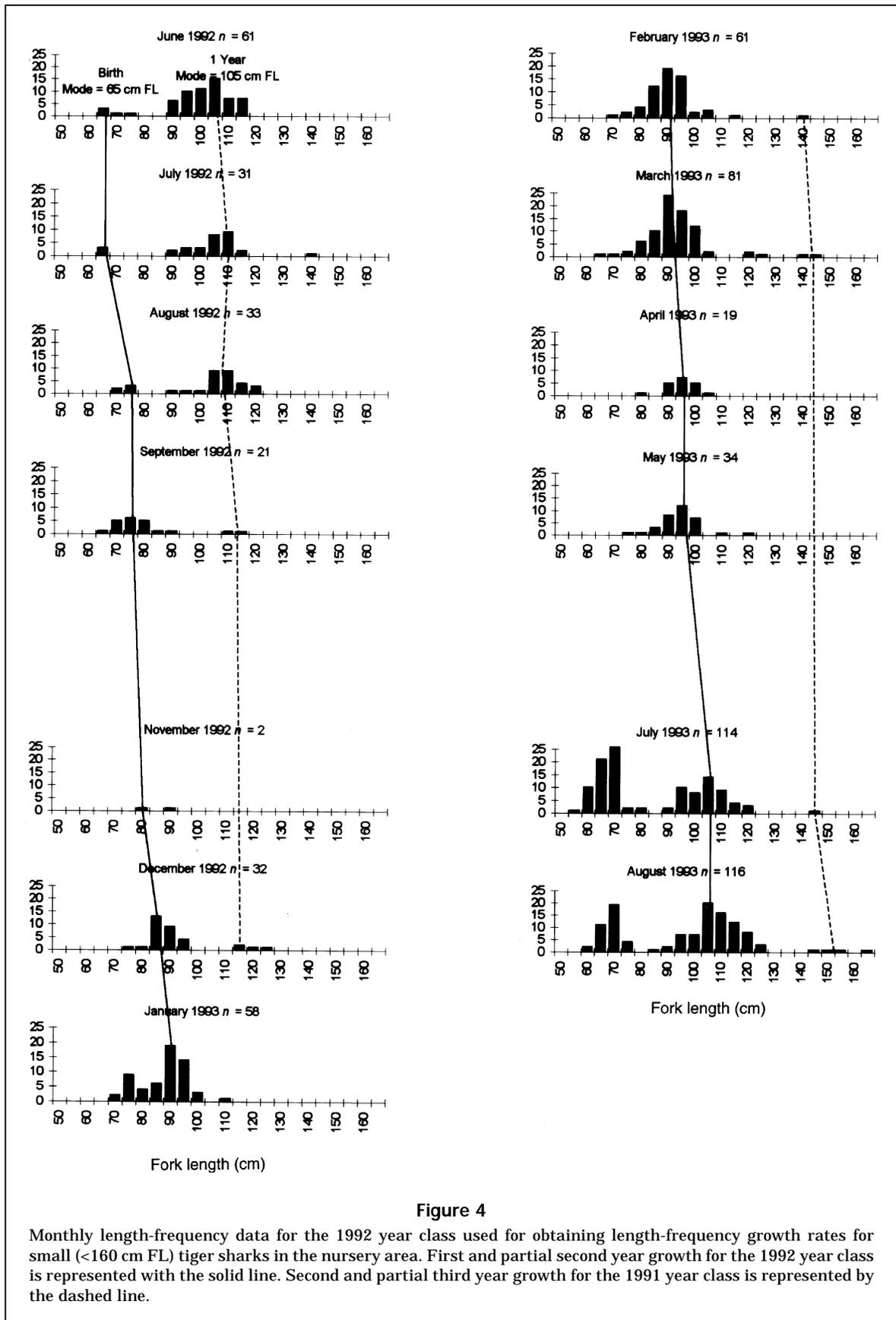


Figure 4

Monthly length-frequency data for the 1992 year class used for obtaining length-frequency growth rates for small (<160 cm FL) tiger sharks in the nursery area. First and partial second year growth for the 1992 year class is represented with the solid line. Second and partial third year growth for the 1991 year class is represented by the dashed line.

Casey and Natanson (1992) showed the advantage of using tag-recapture data over vertebral analysis for aging the sandbar shark. Cailliet et al. (1986) reviewed the techniques available for determining age and verifying age estimates in elasmobranchs. They pointed out that ages estimated from growth zones in calcified hard parts need to be verified with other methods, such as length-frequency and tag-recapture analyses. The authors also stressed the importance of validating the temporal periodicity of the calcified bands with tag-recapture data from the laboratory or field, coupled with OTC marking. Cailliet (1990), in an update of the Cailliet et al. (1986) review, listed the studies, to that date that had employed the various verification methods. Several of these used the combination of tag-recapture, length-frequency and OTC marking for verification or validation (or both) of the calcified structure age estimates. Growth estimates from a laboratory and field study of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Branstetter 1987a) corresponded well to estimates generated with length frequencies and vertebral rings (Parsons, 1985). Casey et al. (1985) used length-frequency, vertebral and tag-recapture analyses to verify age estimates for the sandbar shark, *C. plumbeus*, and concluded that there was close agreement with all three methods. Pratt and Casey (1983) also used these three methods to age the shortfin mako, *Isurus oxyrinchus*, and concluded that not only was there agreement between the methods but that tagging did not affect growth in this species. Smith (1984) validated the periodicity of vertebral band deposition in the leopard shark, *Triakis semifasciata* using OTC. Kusher et al. (1992) were able to confirm these results as well as use length-frequency data and additional tag-recapture data to produce independent age estimates for this species. The tag-recapture curve gave slower  $k$  values than the vertebral, and although the  $k$  values were not significantly different, the authors suggested that tagging may have had an effect on growth in this species (Kusher et al. 1992). These results accentuate the requirement of good tag and recapture data as a backup for vertebral studies, particularly if combined with OTC injections for validation. In the case of the tiger shark in this study, tag-recapture and length-frequency data have provided independent estimates of growth for verification. In addition, the results present evidence against the suggestion that tagging, with or without OTC injection, decreases the growth rate of sharks. It can be argued that the tiger shark cannot be used to generalize about sharks because they grow rapidly in relation to many other species. A birth size of 61 cm FL with a corresponding weight of 1.8 kgs. is small in

relation to many large coastal species, such as the dusky shark (size and weight at birth: 81 cm FL and 7 kgs., respectively, Castro, 1983; Kohler et al., 1995) and the silky shark (size and weight at birth: 64 cm FL and 9 kgs., respectively). If these relatively small tiger shark young can withstand the rigors of tagging and continue to grow at a similar rate as untagged individuals, then it is certainly reasonable to believe that a larger shark can as well. Regardless, all species need to be evaluated individually for their reactions to tagging and OTC injection.

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